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THE POPULATION BIOLOGY OF THE NEOTROPICAL SATYRID BUTTERFLY, *EUPTYCHIA HERMES*.

I. INTERPOPULATION MOVEMENT, GENERAL ECOLOGY, AND POPULATION SIZES IN LOWLAND COSTA RICA (DRY SEASON, 1966).

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NO THOROUGH STUDY OF LEPIDOPTERAN POPULATION STRUCTURE in the Neotropics has been done, yet the butterflies reach their greatest diversity in this biogeographic realm. The present investigation of *Euptychia hermes* Fabricius (Satyridae) is the first to involve a neotropical satyrid butterfly, and because the species ranges north to the Atlantic coast of the United States the choice of this *Euptychia* will allow future comparisons of the structure of both temperate and tropical populations of the same species. Reported here are data obtained on population size and intrapopulation and interpopulation movement in populations of *E. hermes* located in western and eastern Costa Rica, in Central America.

MATERIAL AND METHODS

Euptychia hermes is a small satyrid, dull brown in ground color, and with a wingspread of about 25 mm. The sexes are similar in coloration and pattern. On the undersides of the wings are several reddish-brown lines (submarginal and limbal positions) and a number of marginal ocelli. The ocelli are rather indistinct on the forewings, but on the hindwings, six well-marked ocelli are present (Figure 1). The degree of development of these hindwing ocelli was used as an index to phenetic variation (data to be reported later).

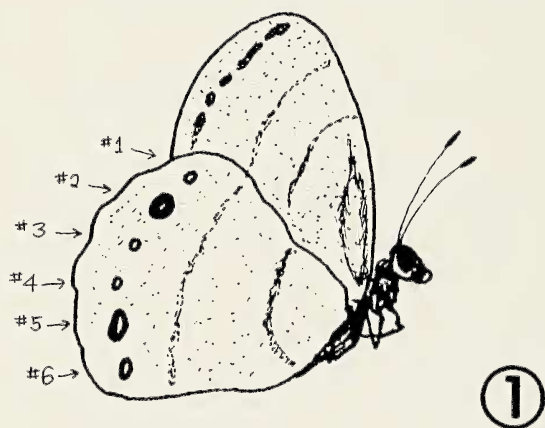


Fig. 1. *Euptychia hermes*: ventral surface, showing ocellation pattern.

A capture-mark-release-recapture program to determine population size and extent of individual movement was carried out in a series of populations in Guanacaste Province (four successive days) and in one population in Limón Province (six successive days). Magic-Marker ink pens were used to mark the individual butterflies on the wings by a code system (Ehrlich and Davidson, 1961). As this butterfly was found to be most active in the early morning, all marking studies were done between 7:00 and 9:30 a.m. and repeated daily. Each area was sampled once a day to avoid the complication of same-day recaptures. All butterflies flying in a population could be captured in 30 to 40 minutes at most, and the earlier captures were retained in extra nets until that time when all specimens were marked (or recorded if a recapture) and then released again.

DESCRIPTION OF STUDY AREAS

I. Guanacaste Populations (Western Costa Rica):

A series of five populations were located along a thousand-foot (300+ meters) section of the river road east of the experimental station of the Costa Rica Ministry of Agriculture and Livestock, adjacent to the Finca Taboga, located 13.5 km. southeast of Cañas, Guanacaste Province, at an elevation of 11.5 meters (38 feet) above sea level. The study was carried out February 13-16, 1966.

The general vegetational formation was dry tropical deciduous forest, in a late stage of second-growth recovery along the road where a series of grassy "islands" were surrounded by vine-covered shrubs and dense undergrowth except on the road side, and were isolated from each other by differing expanses of dry habitat. The small meadows were bordered on the east by a swamp, the source of moisture for the green grasses. *Euptychia hermes* at this location was abundant in these grassy areas; individuals were occasionally encountered elsewhere in the dry forest. The entire group of colonies in the study area was isolated from other grassy regions along the road by at least 250 feet (70 meters). Figure 2 shows the spatial orientation of the population sites.

The grasses were one-third to one-half meter in height; the surrounding vines and shrubbery were 1.5 to 2 meters and more in height. The butterflies flew over these latter "barriers" on occasion, but usually flew *into* them through slight "holes" in the leafy wall, when pursued or when the sun rose higher in the late morning. Second-growth plants found in the study area

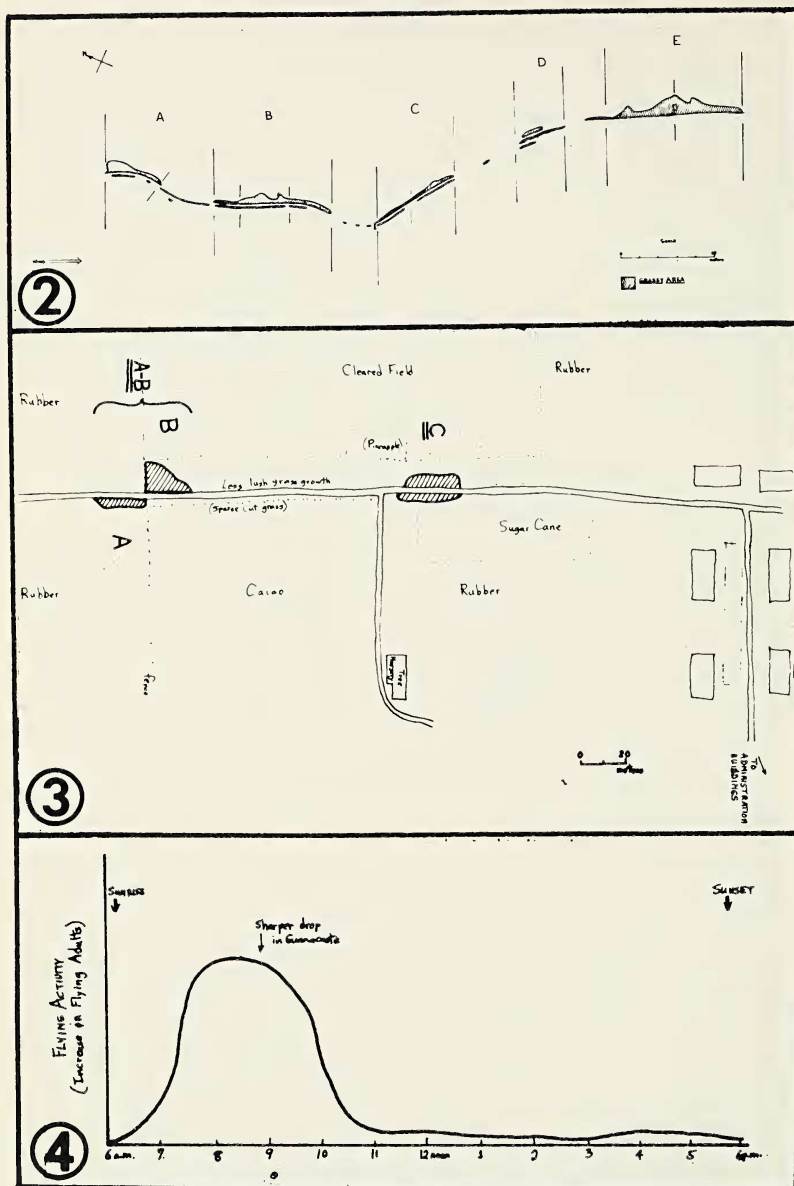


Fig. 2. The spatial orientation of the population sites studied along the river road on the Finca Taboga, southeast of Cañas, Guanacaste Province, Costa Rica.

Fig. 3. Map of the population areas studied on the Los Diamantes experimental station grounds, east of Guápiles, Limón Province, Costa Rica.

Fig. 4. Daily fluctuation in flight activity of *Euptychia hermes* at the low-land Costa Rican study sites: open meadow populations.

were: *Solanum* (3-4 meters high, a border tree), two species of *Salvia* (Labiatace), *Oenothera*, *Cassia* (a border tree), several species of vines (Convolvulaceae and Vitaceae), *Philanthus* (Euphorbiaceae, a border plant), *Triplaris* (a border tree), *Panicum* grass) and two unidentified grasses (one of which the butterfly flew around and frequently landed on).

The daily weather here was sunny and hot with intermittent clouds. During the hours of the capture-recapture studies, the temperature ranged from about 75 to 86°F., a daily maximum of 96 to 98°F. was usual. The relative humidity was around 50%. A strong gusty wind developed by 9:15 a.m. every day.

II. *Los Diamantes Populations (Eastern Costa Rica):*

The capture-recapture study was done March 4-9, 1966, on a population inhabiting a lush grassy area surrounded by cleared fields and cacao and rubber plantations (these areas with grasses also), located about a half kilometer northeast of the buildings at the Los Diamantes experimental station of the Costa Rican Ministry of Agriculture and Livestock, 1 km. east of Guápiles, Limón Province, at an elevation of 300 meters (984 feet). An adjacent population was sampled to study local variation patterns (see Figure 3 for map).

The grasses were lush on the east side of the road and up to 35 cm. in height; many *Euptychia* were flying here. On the west side of the road, the grass had been cut short and few butterflies occurred there. In Area C, many *Euptychia* were landing on crushed sugar cane stalks in the road and sipping the sap. The peak of butterfly activity, as at Guanacaste, was between 7:00 and 9:30 a.m. The daily weather was warm, from about 72 to 80° during the capture-recapture periods, and up to 86° or so as a daily maximum. Partly to completely cloudy skies, with occasional showers, were the rule. Relative humidity ranged from 85 to 100%.

A small sample of adults from the nearby and largely uncut rain forest, 8 km. west of Guápiles (by the Río Toro Amarillo), was taken; the butterflies were very scarce and scattered there, despite apparently satisfactory grassy areas along the roads.

GENERAL BIOLOGY & ACTIVITY OF *EUPTYCHIA HERMES*

When the first morning sun hits the grassy site of a population around 7 a.m., the *Euptychia* begin flying. During the following two hours, they are quite active and drink sap from crushed

sugar cane and suck water from mud in the road bed. By 9:30 a.m., when the full sun is quite intense, there is hardly a butterfly to be seen in the open. This lack of activity in open areas continues through the rest of the day. In Guanacaste, it was noted that a few were flying in the shade or in the undergrowth, wherever they were protected from the sun and partly protected from the strong winds. The daily activity cycle is roughly graphed in Figure 4.

This *Euptychia* is a low-flying butterfly, clearing the ground or tops of grass blades by only a few inches. It frequently rests on the broad-bladed grasses. No oviposition was observed. No evidence of larvae could be found, but this is usual for satyrid populations because of the nocturnal larval feeding habits and the known behavior in several nearctic satyrids of eating the entire grass blade, leaving little or no evidence of activity.

One mating attempt was observed at 8:45 a.m. February 14 at Guanacaste. A female landed on a partially-sunlit horizontal grass blade and a male, which had been following her closely in flight, landed behind her. He walked rapidly up on her left side and curved his abdomen around in a U-shape into a copulating position, but the female was skittish and moved away slightly. At this point, a second male landed ahead of the female and rushed towards the pair; all three butterflies immediately flew away in separate directions.

Euptychia hermes was sympatric with three other *Euptychia* species at Guanacaste, and with one of the same species at Los Diamantes in Limón Province.

Analysis of the age composition (as determined by fresh, intermediate or worn conditions of wings, and the daily addition of fresh adults) of the male and female samples of all populations indicated a continuous emergence well before and during the study period in both the western and eastern populations. There is no reason to doubt the belief that this *Euptychia* breeds continuously throughout the year in these lowland forests (surprisingly even during the dry season in the deciduous forest, wherever moisture for green grass is available), as larval food is apparently available at all seasons and the species is known to occur at all seasons in tropical parts of eastern Mexico (Emmel, unpublished data). Therefore the species probably does not have a diapause stage in these tropical populations. It would be of interest to carry out comparative physiological and genetic studies with *E. hermes* since the extra-tropical populations in the north, which face severe conditions with a cold winter instead

of a dry season, apparently have a genetically controlled, obligatory diapause in the larval stage.

A red Orbatid mite was found on the dorsal surface of the abdomen on each of two females in the Los Diamantes area; these mites were firmly attached and feeding. No bird attacks or other predation were observed. No flower-feeding by the adults was ever noted, so it is unlikely that reduviid bugs, mantids or crab spiders are significant predators.

POPULATION SIZE ESTIMATES

I. Guanacaste Results:

During the first three days, 59 adults were marked and released, with 32 new adults added in sampling on the fourth and final day of study. Of the 59 releases, 7 (3 males, 4 females) were recaptured at least once, 1 female was recaptured twice, and 1 female was recaptured on all three days following the day it was marked. No marked butterfly changed from one population area to another. Only one individual was recaptured in a marked population other than E, so estimates of population size (total number of individuals flying daily) were restricted to population E, using a simple Lincoln-Index proportion calculation.

<i>Est. Population Size</i>	<i>Date</i>
110 adults	February 14
75 adults	February 15
234 adults	February 16

Allowing for vagaries of individuals and varying weather conditions, these figures give an approximate population size of between 75 and 250 adults for a grassy area of only about 30 square meters. It is likely that individuals move back into the undergrowth in daily wanderings and may be absent from the grassy stand for a day or two. Variations in apparent flying-adult population size are known to be due to these environmental and "wandering" factors, among others (Emmel and Emmel, 1963).

II. Los Diamantes (Limón Province) Results:

A total of 57 adults were marked and released in population A-B during the first days of the study; three more were sampled on the sixth day. Of the 57 releases, 8 were recaptured once; none was recaptured twice. The marked irregularity of recapture of marked adults (none on three days) permits estimates for only the following three dates:

TABLE 1
Sex Ratios in the Guanacaste Populations:
Daily New Captures (1966)

Population	Feb. 13		Feb. 14		Feb. 15		Feb. 16		Population totals	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
A	-	-	2	0	-	-	-	-	2	0
B	3	0	2	0	1	0	1	0	7	0
C	-	-	4	2	6	3	6	1	16	6
D	-	-	-	-	-	-	2	1	2	1
E	4	6	10	10	3	3	16	6	33	25
Daily Totals:	7	6	18	12	10	6	25	8	60	32
									(92 adults) Ratio=1.88:1.00, ♂: ♀	

<i>Est. Population Size</i>	<i>Date</i>
109	March 6
299	March 8
143	March 9

Since individuals were frequently seen entering and leaving Area A-B, and since all but one recaptures were females (and females are notably more sedentary than males in this and all other butterfly species studied to date) and none was recaptured more than once, it seems probable that this supposed "population" is merely a concentration of individuals in a section of a much larger population, whose individuals range into the rubber groves and adjacent fields for at least 30 meters or more (observed distance of flight of several males). This lush grass area is also likely a favored oviposition site for the females (note the preponderance of females here, in Table 2, as compared to the "normal" preponderance of males in Population C and in Guanacaste populations).

SEX RATIO IN POPULATIONS

The overall sex ratio in the Guanacaste populations was 1.88 males: 1.00 female (Table 1). Most females occurred in population E here, which apparently was the only stable resident population in view of the capture-recapture results.

In the Los Diamantes populations, the overall sex ratio was 0.95 males : 1.00 female (Table 2). When the transient "population" A-B (sex ratio of 0.58 : 1.00) is considered separately from the apparently "resident" population C, though, the latter (sex ratio of 1.41 males to 1.00 females) is seen to be similar in its male-dominated sex ratio to the Guanacaste populations.

EXTENT OF INTRA- AND INTER-POPULATION MOVEMENT

There was no observed interchange of individuals between any of the Guanacaste populations (delineated by shaded areas on the map in Figure 2); thus these appear to be reproductively isolated breeding units. The same conclusion is reached for the Limón populations from the lack of interchange of marked individuals between Area A-B and Area C at Los Diamantes. From the available evidence, then, a distance of several score meters or less (only 20 meters between areas A and B in Guanacaste) of unsuitable habitat appears to effectively separate populations of this *Euptychia* species. Further study is needed here to de-

termine the precise amount and type of barrier required for isolation; quite likely, the barriers to dispersal are intrinsic (genetically-controlled) as well as environmental, since this butterfly is capable of flying over thirty meters when pursued and can fly through tangled undergrowth without much hesitation.

The marked butterflies in subareas E_1 and E_2 of the Guanacaste Population E, and in subareas A and B of the Los Diamantes Population A-B, exchanged daily positions back and forth within the total population area with equal frequencies. From observation of flight behavior, also, there was no evidence of territorial or homing behavior in either males or females. This is in contrast to data obtained on the nearctic lycaenid butterfly, *Plebejus icarioides*, where both sexes usually stay in their "home" part of the population area and will return to it if displaced (Emmel, ms, in prep.).

DISCUSSION AND CONCLUSIONS

The general findings of the present study concur with many population parameters characteristic of the majority of investigated temperate-zone butterflies. This *Euptychia* exhibits about the same degree of sedentary behavior as the satyrid *Cercyonis oetus* (Emmel, 1964, unpublished); the lycaenids *Plebejus icarioides* (Emmel, ms. in prep.), *Philotes sonorensis* (Mattoni and Ralston, ms. in prep.), and *Polyommatus icarus* (Dowdeswell et al., 1940); the nymphalid *Euphydryas editha* (Ehrlich, 1961, 1965); and the pierid *Anthocaris sara* (Evans, 1955). In other words, the species fails to exercise its apparently high degree of vagility, the ability to cross barriers. Capture-mark-recapture studies confirmed that while intrapopulation movement occurs regularly, interpopulation movement is of such insignificance that these populations are effectively genetic isolates, despite being separated, in some cases, by only about twenty or thirty meters of unsuitable habitat.

The species is most active in the early-morning hours and the later decrease in flight activity may be due to wind (at Guanacaste) and solar radiation reaching relatively intolerable levels as the day progresses. *Euptychia hermes* most likely breeds continuously throughout the year in these tropical populations, even in areas having a pronounced dry season. One might suppose that populations increase and disperse to make essentially continuous huge populations in many areas during the wet season, when more green grasses would be available. However,

the fact that such large continuous populations were not found in the eastern wet rain forest areas mitigates against this hypothesis. Since the distribution of the species in lowland Costa Rica seemed closely tied to that of a certain broad-leafed grass (still to be identified), foodplant specificity may control the butterfly's distribution more than any particular environmental factor. Such a situation is suspected for the satyrid *Cercyonis meadi* in the western U.S., which occurs in widely-scattered, small populations from 5000-foot-elevation juniper woodlands to 10,000-foot-elevation mountain pine forests, always in association with particular grass species (Emmel, unpublished).

SUMMARY

Population sizes, intrapopulation and interpopulation movement, and local and geographic phenetic variation were analyzed in grassy meadow populations of the satyrid butterfly, *Euptychia hermes* Fabricius, located in western and eastern Costa Rica (Finca Taboga, Guanacaste Province; and Los Diamantes, Limón Province). Population size was determined by mark-recapture experiments; a typical population site of 30 square meters in area had between 75 and 250 flying adults in it during the dry-season study period.

No movement of marked individuals occurred between populations separated by as little as 20 meters of dry or non-grassy areas, yet the butterflies moved freely around within a population area and when deliberately forced to, could fly more than 30 meters linear distance. Thus, intrinsic (genetic) factors probably play the major role in limiting flight movement and dispersal.

ACKNOWLEDGMENTS

This research was carried out while the author was a participant in the Organization for Tropical Studies Fundamentals of Tropical Biology course, February-March 1966, in Costa Rica. Dr. Charles D. Michener, University of Kansas, kindly reviewed and commented upon an earlier draft of this manuscript. The present version is the first of a series of papers analyzing tropical and temperate population characteristics in *Euptychia hermes* under the support of a Biomedical Sciences Grant from the Division of Sponsored Research, University of Florida.

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